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RESEARCH PAPER

# Research advances on the biological effects of elevated ultraviolet-B radiation on terrestrial plants

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**Abstract:** This review describes the effects of ultraviolet-B (UV-B) radiation on plant growth and development, photosynthesis and photosynthetic pigments and UV-B absorbing compounds. Moreover, plant ecosystem level responses to elevated UV-B radiation and interactions of UV-B radiation with abiotic and biotic factors were also involved. Results collected in this review suggest that approximately two-thirds terrestrial plant species are significantly affected by increase in UV-B radiation. The majority of evidences indicate that elevated UV-B radiation is usually detrimental but there exists tremendous variability in the sensitivity of species to UV-B radiation, and sensitivity also differs among cultivars of the same species.

**Keywords:** ultraviolet radiation; ozone depletion; photosynthesis; environment stress

## Introduction

Ozone is a strong absorber of solar ultraviolet radiation, and the stratospheric ozone layer acts to filter out much of the ultraviolet component of the solar spectrum before it reaches the earth's surface. However, a reduction of the stratospheric ozone layer has taken place over the last several decades in response to chlorofluorocarbons emissions from mankind's activity, which have been well documented (WMO 2007). Depletion of ozone resulted in a substantial increase in the UV-B radiation (280–320 nm) reaching the earth's surface.

UV-B radiation effects on terrestrial plants involve in the molecular scale, such as DNA damage, tissue and whole plant scale, including a decrease in photosynthetic activity and changes in plant structure and biomass, and the communities and ecosystems scale, including a possible shift in competitive balance between species and species populations. When exposed to elevated UV-B radiation, plants present a wide variety of physiological and morphological responses characterized as acclimation and adaptation, which is now of major concern to biologists because these responses potentially threat to productivity of agriculture and forestry, as well as to the stability of terrestrial ecosystem. For example, the measured physiological and biochemical parameters on pea and wheat indicated that UV-B radiation has a stronger stress effect than drought on plant growth (Alexieva et al. 2001). Therefore, since the first report revealed potential stratospheric ozone reduction in 1970's (Johnston 1971), considerable researches on the biological effects of increased solar UV-B radiation on terrestrial plants have been conducted worldwide (Caldwell 1971).

Great numbers of reports indicate that most terrestrial plants could potentially be affected by increased solar UV-B radiation, including plant morphology, biomass and seed production, secondary metabolites, disease incidence and population fluctuations, et al. However, there exists tremendous variability in plant species sensitivity to UV-B radiation (Teramura 1983). Some species show sensitivity to present levels of UV-B radiation while others are apparently unaffected by rather massive enhancements (Becwar et al. 1982). This issue is further complicated by reports of large response differences among cultivars of a species (Feng et al. 2002).

In this paper, recent advances in studies on the UV-B biological effects on plants from a great deal of literatures were overviewed. We concentrated on the impact of elevated UV-B radiation on terrestrial plant morphology, photosynthesis and photosynthetic pigments, DNA damage and biomass productivity, as well as on the terrestrial ecosystem function and stability. Finally the future study hotspots in fields of UV-B effects on terrestrial plant were summarized.

## General effects on organisms

### Effects of UV-B radiation on plant morphology

Numerous studies have been conducted to determine the impacts of UV-B radiation on plant morphology and growth allocation. The responses to UV-B treatments under field conditions involved in substantial changes in plant morphology and development, including plant height, leaf area, leaf thickness, branching

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and plant phenology. Among morphology characteristics altered by UV-B radiation, reductions in plant height and leaf expansion are most pronounced. Inhibition of stem elongation and leaf area expansion has been observed in many species in response to elevated UV-B radiation (Caldwell et al. 1995), which lead to more compact and shorter plants. For example, UV-B exclusion experiments in the field with the *Datura ferox* L. suggested that elevated UV-B incident reduced seedling emergence, inhibited stem elongation and leaf expansion, and tended to reduce biomass accumulation during early growth periods (Ballaré et al. 1996). In the study conducted by Tevini et al. (1991), plant height, leaf area, and the dry weight of sunflower, corn, and rye seedlings were significantly reduced with elevated UV-B radiation. Delays in development and decrease in plant height were also observed at early tillering stage of spring wheat with elevated UV-B treatment (Li et al. 1998). Mark and Tevini (1996) speculated that the mechanism for reduced stem elongation by elevated UV-B radiation might be due to changes in the phytohormone levels, especially IAA which plays a role in stem elongation.

Similar to plant height, leaf area is also a very sensitive growth parameter that responds to elevated UV-B radiation. Leaf area was less due to both smaller and lesser number of leaves when plants were exposed to elevated UV-B radiation (Zhao et al. 2003). The reduction in leaf area was caused by a reduction in cell size and a change in leaf structure (Hofmann et al. 2001). On the other hand, increase in leaf thickness due to their anatomical response to UV-B radiation was often reported (e.g., Bornman and Vogelman 1991). Yamasaki et al. (2007) reported that continuous UV-B irradiation on the surface of cucumber cotyledons induced cell division at or under the basal part of sharp-headed trichomes, resulting in an increase in the number of cell layers from three to six. In contrast to these findings, some studies also reported a decrease in leaf thickness along with an increase in number of palisade layers under elevated UV-B radiation, for example, the field studies on cotton revealed a decrease in thickness of both the palisade and mesophyll tissue, while the epidermal thickness remained unchanged (Kakani et al. 2003).

## Effects of UV-B radiation on photosynthesis and photosynthetic pigments

One of the most susceptible physiological processes of plant to elevated UV-B radiation is photosynthesis. Many studies indicated that elevated UV-B radiation resulting in a decrease in photosynthetic activities, though these responses depend on plant species, cultivars, experimental conditions and UV-B dosage. Battaglia and Brennan (2000) reported that treatment with UV-B radiation of 194 $kJ \cdot m^{-2}$ lead to significantly reduced cotyledon $CO_2$ fixation rates in cucumber, but no such effect in sunflower. Correia et al. (1999) found that under field conditions, a 30% increase in UV-B radiation from ambient level significantly decreased leaf photosynthesis of most corn cultivars (25%–46%), but the photosynthetic rates of two cultivars did not change, compared to the control. A pot experiment conducted by Cai et al. (2007) in the field showed that the photosynthetic responses of pioneer plants to elevated UV-B radiation were greater than those of species in late successional stage, which suggested that the late successional stage species were more tolerant to UV-B radiation, and therefore, could compete for more resource to keep dominance in ecosystem.

Currently it is not clear about the mechanism of photosynthesis inhibition induced by UV-B radiation. Decreases in Rubisco activity, stomatal conductance and PSII activity have been reported as possible candidates. Ultrastructural damage to chloroplasts and changes in photosynthetic pigments also result in reduction of photosynthesis. Changes in leaf ultrastructure due to elevated UV-B radiation would modify the light penetrability of leaf and hence affect photosynthesis. A decrease in chlorophyll content was evident on exposure to elevated UV-B radiation in most of the plant species due to a breakdown of the structural integrity of chloroplasts. Chlorophyll reduction on exposure to UV-B in major plant species ranged from as low as 10% to as high as 78% (Kakani et al. 2003) and the reduction being higher among the dicot species, compared to that in monocot species, which in some ways explains plant species differed in their ability to tolerate UV-B radiation.

UV-B radiation can have a deleterious effect on several targets of photosynthetic organisms. The most UV-B sensitive organism is the light energy-converting complex of photosystem II (PS II) (Andersson et al. 1991). Inhibition of PSII activity by UV-B radiation is accompanied by the degradation of the D1 and D2 protein subunits, which form the heart of the PS II reaction center by contributing ligands to cofactors that mediate primary photochemistry. The mechanism of damage induced by UV-B radiation to the electron transport and protein structure of PSII has been investigated by a number of studies. According to a widely accepted viewpoint, UV-B radiation mainly damages the donor side of PSII by inactivating the Mn cluster of water oxidation (e.g., Post et al. 1996). For example, Vass et al. (1996) found that UV-B irradiation results in the rapid inhibition of oxygen evolution and the decline of variable chlorophyll fluorescence. UV-B irradiation also induces the degradation of the D1 reaction center protein. These effects are accompanied by the loss of the multiline EPR signal arising from the S2 state of the water-oxidizing complex. Sicora et al. (2003) proposed that photoinhibition by sunlight can be initiated by a UV-B induced inhibition of PSII donor side followed by the destruction of the PSII reaction center. This idea was developed by Bergo et al. (2003) who declared that the formation of the C-terminal fragment of D1 protein fragment in UV-B light is a photochemical process, whereas the degradation of the fragment in white light is a protease-mediated process.

## Effects of UV-B radiation on plant protective mechanisms

UV-B radiation produces several detrimental effects on plant cells, including damage to proteins, membrane lipids, and DNA. Plants have developed natural adaptations such as anatomical, morphological and biochemical changes, which help to reduce UV-B penetration into plant tissues, and to alleviate the detrimental effect of UV-B radiation. It has been reported (Ballaré et al. 1995) that the inhibition of hypocotyl elongation and retardation of plumular hook opening in emerging seedlings increased amount of UV-B-absorbing compounds in the epidermis, thereby reducing the damaging impact of UV-B when the seedling eventually is exposed to full sunlight. Similarly, the reduced leaf area expansion and increased leaf thickness induced by elevated

UV-B radiation may lengthen the optical path between the leaf epidermis and sensitive cellular sites in the mesophyll. The palisade cells from UV-B irradiated leaves were wider and shorter. The increase in cell number would increase the cell wall surface area, which blocks and prevents the harmful UV-B radiation from reaching the abaxial photosynthetically active mesophyll. The increased palisade cell number would also increase the amount of air-cell wall interfaces, which is an important parameter affecting reflectance and transmission of the incident radiation through the leaf surface (Bornman and Vogelman 1991).

In UV-B supplementation studies, an increase in production of secondary metabolites in leaf tissues was the most apparent response across studies. These studies indicated that UV-B absorbing compounds increase from 10% to 300% in plants. Sedej and Gaberscik (2008) argued that the tolerance of Norway spruce to elevated UV-B radiation was to a large extent due to the high content of methanol-soluble UV-B absorbing compounds. Li et al. (1993) demonstrated that both flavonoids and other phenolic compounds play important roles in the protection of plant from elevated UV-B radiation. Steinmuller and Tevini (1985) found that elevated UV-B irradiation produced 23% and 28% increase in wax content on leaf area from barley and bean, respectively. The epicuticular wax layer is known to accumulate most of the secondary metabolites, such as phenolics and flavonoids that absorb UV-B radiation and shield the underlying tissues against harmful UV-B radiation (Olsson et al. 1998). Besides, epicuticular wax increases reflectance markedly in the ultraviolet and blue regions of the spectrum. For example, increased wax provided a protective mechanism as the epicuticular wax reflects from 10% to 30% of the incident UV-B radiation in eucalyptus (Holmes 1997).

### Effects of UV-B radiation on DNA damage

One obvious target for UV-B induced damage to plants is DNA. The biological effects of UV-B radiation on plants included both changes at the physiological level and more direct damage to cellular macromolecules such as DNA. Several types of damage can occur as a result of absorption of UV-B photons by DNA. Ballaré et al. (1996) reported that leaves of *Datura ferox* that received near ambient UV-B levels had about twice the number of lesions per unit of DNA more than plants grown with UV-B exclusions. Rousseaux et al. (1999) found that the passages of the ozone hole over South America caused concomitant increases in UV-B radiation and led to significant increases in DNA damage in the native plants. The fluctuations in solar UV-B radiation explained a large proportion of the variation in DNA damage (up to 68%).

The mounting evidences have shown that direct and indirect damaging effect of UV-B radiation on plants DNA could be a concrete threat to terrestrial ecosystem. Several studies suggested the inhibition of stem elongation is either a direct consequence of damage to proteins or is somehow a cellular signal derived from DNA damage by UV-B radiation (Beggs et al. 1985). A letters to journal *Nature* pointed out that increases in terrestrial solar UV-B radiation as forecasted for the early 21st century may affect genome stability in plants, but the good thing is that the damaged DNA could be repaired correctly so that mutations are avoided and the genome can remain functional (Ries et al. 2000).

In recent years, UV-B radiation caused DNA damages and repairs have been intensively studied (Kimura and Sakaguchi 2006). A number of studies are currently attempting to identify the genes required for UV-B tolerance and repair. Studies of *in vivo* cellular repair mechanisms have focused largely on DNA repair by themselves in plants (e.g., Machado et al. 1996). It is conceivable that some plants have evolved particularly efficient mechanisms for the elimination of UV-induced DNA damage (Britt 1995). Usually plants have the ability to repair DNA damages caused by UV-B irradiation, using DNA repair enzymes such as photolyase. However, the repair capability is very slow depending upon the plants themselves. It was reported that high photosynthetically active radiation (Olszuk 1996), high concentration of $CO_2$ (Teramara 1990) and low nitrogen supply (Hunt and McNeil, 1998) could alleviate cells damage caused by UV-B radiation in plants.

Past studies have illustrated that laser pretreatment could protect plant cell from elevated UV-B radiation (Qi et al. 2000)). Though the mechanism of the bio-effect of lasers is not explicit, it led to the hypothesis that lasers have the ability to repair or accelerate repair of plant damage induced by UV-B radiation. Through a series of experiments on broad bean (*Vicia faba* L.) using He–Ne Laser, Qi et al. (2002) reported that the laser had a long-term positive physiological effect on the growth of UV-B–damaged plants. With the exception of the severe damage caused by higher UV-B radiation, a laser with the proper flux rate and treatment time can repair UV-B–induced damage and shorten the recovery time. Similar results were obtained by Han et al. (2002) in a study with wheat. Qiu et al. (2006) first reported the optical effect of a semiconductor laser on protecting wheat from UV-B radiation damage, and demonstrated that semiconductor laser irradiance had the capability to protect plants from UV-B-induced DNA damage. Although some progresses have been made in the genetics of DNA damages repairs, the studies on higher plants is still in its infancy. The difficulty is that the DNA repair is not only a fundamental cellular process for protecting cells against the damage, but is also essential to ensure faithful transmission of genetic information from one generation to the next. It would be useful to know more about DNA repair mechanisms, capacity, and what enzymes repair what kinds of damage.

## Interaction of UV-B and other environmental factors

Plants in nature are seldom affected by a single stress factor. Instead, they typically respond to several factors acting in concert, such as water stress, increased $CO_2$ concentration, availability of nutrients, altered precipitation and temperature (Caldwell et al. 1998). The changes of other environmental factors are likely to modify the impacts of UV-B radiation on plants, while in turn varied UV-B radiation can alter the way in which plants respond to environmental factors. Several factors have been shown to modify UV-B-induced responses of plants, either alleviating or enhancing the UV-B radiation effect. However, concurrent responses of terrestrial plants to the combination of elevated UV-B radiation and other factors, such as temperature, $CO_2$, available nitrogen, and water supply are less well understood.

Under the background of global climate change, there is growing interest regarding the joint effects of elevated UV-B radiation and other environmental factors on plants. On the other hand, though the interactive effects between these abiotic or biotic factors and UV-B radiation has been recognized as important in the prediction of global climate change, there have been relatively few studies that have examined the joint effects of UV-B and other stress factors on plant response. Available study results showed both positive and negative interactive effects on plants with UV-B radiation along with other environmental factors. The overall UV-B effect was aggravated and in some cases ameliorated by environmental factors (Caldwell et al. 1998).

Interactive effect of UV-B and $CO_2$

When studied independently, plant growth can be augmented by elevated $CO_2$ levels, while plant growth responses to elevated UV-B radiation generally presents an opposite directions. Many earlier studies have shown that elevated $CO_2$ ameliorates many injurious effects of UV-B and very few aggravated cases were reported. For example, using canola under controlled environment conditions, Qaderi and Reid (2005) found that elevated $CO_2$ concentrations counteract the tendency of decreasing plant height by UV-B radiation. Elevated $CO_2$ sometimes appears to provide some protection against elevated UV-B radiation for some species; however, several newest studies suggested that many of the damage effects of UV-B radiation are usually not ameliorated by the elevated $CO_2$. For example, Koti et al. (2005) reported that elevated $CO_2$ had a small beneficial effect in some soybean varieties, but didn't alleviate the detrimental effect of high UV-B radiation on pollen morphology, production, or germination. Similar results were also obtained for supplemental UV-B radiation and elevated $CO_2$ concentration in an experiment on cotton (Zhao et al. 2004).

Interactive effect of UV-B and water stress

Plants that endure water deficit stress effectively are likely to be tolerant to high UV-B radiation. Paoletti (2005) found that Mediterranean forest species are well protected against increases in UV-B radiation due to long term natural adaptations to water stress. Through experiments on two contrasting poplar species, Ren et al. (2007) also found that plants originating from high altitude and being apparently adapted to drought and high levels of UV-B, exhibit greater tolerance to drought and elevated UV-B radiation than plants from lower altitude. Initially the interpretation was that water stress resulted in a large reduction in photosynthesis and growth that masked the UV-B effect, but now it tended to be explained as that water-stressed plants resulted in a higher concentration of leaf flavonoids, which in turn, provided greater UV-B resistance (Ren et al. 2007).

Similarly, elevated UV-B radiation in field experiments tended to alleviate drought symptoms. Interaction experiments on spring wheat suggested that co-stresses of supplementary UV-B radiation and drought synergistically functioned and one of them could alleviate the inhibitory effects of another under the condition of arid and semiarid (Feng et al. 2007). With shrub from the Tibetan Plateau of China, Yang et al. (2005) found that elevated levels of UV-B radiation tended to alleviate the effects of drought on decreased plant dry mass, and increased the levels of a plant hormone (abscisic acid) that is known to mediate plant responses to water stress.

Interactive effect of UV-B and temperature

Extreme temperatures influence the sensitivity of plants to UV-B radiation directly. Tropical legumes exposed to elevated UV-B radiation were less detrimentally affected if they were simultaneously exposed to higher temperatures (Nedunchezhian and Kulandaivelu 1996). In turn, UV-B radiation sometimes increases plant tolerance under extreme high temperature conditions. For example, UV-B radiation increased heat tolerance considerably in cucumber plants grown in growth chambers (Teklemariam and Blake 2003). On the other hand, freezing tolerance is generally increased by UV-B radiation exposure (Dunning et al. 1994). For example, freezing tolerance of jack pine seedlings grew in growth chambers was increased by UV-B radiation and this was linked to induction of secondary compounds in plant tissues with elevated UV-B radiation (Teklemariam and Blake 2004). In contrast to these findings, decline of frost tolerance was also observed for several tree species (fir, interior spruce and yellow-cedar) when UV-B radiation increased above the ambient level (L'Hirondell and Binder 2005). Thus field validation studies conducted over several growing seasons with full temperature ranges are crucial in assessment of plants responses to elevated UV-B radiation.

Interactive effect of UV-B and nitrogen supply

Interactions of nitrogen and UV-B may be more important in regions experiencing nitrogen deposition or in agricultural systems with nitrogen applications. Studies show that plants well supplied with nitrogen are generally more sensitive to UV-B radiation (Caldwell et al. 2007). In field experiments, supplemental UV-B caused reductions in total biomass, nitrogen content and specific pigment concentrations for a South African legume species, but the UV-B effect was much more pronounced if the plants were supplied with supplemental nitrate (Chimphango et al. 2004). In another field study with simulated ozone reduction, net photosynthesis of maize was more affected by UV-B at high nitrogen supply than at low nitrogen levels (Correia et al. 2005). The majority of evidence indicates that the co-stresses of these two factors will be a critical threat to terrestrial ecosystem production and stability considering that the anticipated increase of both UV-B radiation and nitrogen deposition under the global climate change regime.

## Plant ecosystem responses to UV-B radiation level

The direct effects of elevated UV-B radiation on terrestrial plants may lead to indirect effects on ecosystem balance through effects on other biotic components present in the ecosystem, e.g., plant weeds, diseases, insects and nitrogen-fixers. However, predictions of ecosystem consequences of elevated UV-B radiation are complicated because species interactions and the ecosystem components are also affected by the biotic and abiotic factors, e.g., soils, water, mineral elements, etc.

## Relation between UV-B radiation and plant diseases / insects

Most of our present knowledge about the impacts of elevated UV-B radiation on terrestrial ecosystems comes from studies with plants. Recently, the effects of UV-B radiation on the activities of plant diseases and insects have begun to receive attention. Results from previous experiments indicate that elevated UV-B radiation can significantly increase the susceptibility of plant to disease. Directly, UV-B radiation reduces some plant diseases because of damage to pathogens, which can be a major factor limiting the survival of spores during dispersal and infection period. Indirectly, plant disease could be reduced because UV-B radiation alters the chemistry of the host plants, making it more resistant to infection (Paul 2000).

Insects-plants relationships can also be altered due to the direct effects of UV-B radiation on insect behaviors or the indirect effects on plant secondary metabolites (Caldwell et al. 1989). Actually, changes in plant chemical composition are more commonly reported and may lead to substantial reductions in consumption of plant tissues by insects. Several studies (e.g., Ballaré et al. 1996; Zavala et al. 2001) reported that plants exposed to ambient UV-B radiation often suffer less herbivory by insects than by plants cultivated under filters that specifically exclude the UV-B component of solar radiation. For example, field experiments with *Datura ferox* L. showed that plant exposure to UV-B radiation reduced one-half of the likelihood of leaf attacked by beetle (Ballaré et al. 1996). In a laboratory and field choice experiment with soybean crops, Mazza et al. (1999) found that elevated UV-B radiation strongly reduced thrips herbivory. Thrips preferred leaves from plants that were exposed to solar UV-B radiation, and appeared to avoid exposure to solar UV-B. These experiments suggested that phytophagous insects could present direct and indirect behavioral responses to elevated UV-B. In some ways, it is because of altered insect behaviour, but in most cases, changes in plant chemical and physical characteristics induced by UV-B radiation usually account for the reduced herbivory. Such modifications affect many interactions of plants with other organisms, both above and below ground. This argue was well verified by a climate-manipulation experiment carried out over antarctic vegetation, through the research showed that that near ambient solar UV-B radiation decreased the prevalence of soil-dwelling microarthropod species in soils (Convey et al. 2002). Since these soil insects are not directly exposed to solar radiation, the effects were assumed to have been mediated by UV-B-induced changes in the vegetation.

## Relation between UV-B radiation and species competition

UV-B enhancement may lead to a shift in competitive balance among certain species, such as crops and weeds. Many studies reported that elevated UV-B could alter the competitive balance between crops and weeds (e.g., Barnes et al. 1988), while competition from weeds could reduce crop yield. In a field study with wheat ecosystem, Li and Wang (2001) found with elevated UV-B radiation, species number and population quantity of weeds and soil macroanimals decreased, species diversity changed, total biomass of weeds reduced. Their investigations well revealed that competitive balance between wheat and major weeds could be altered under elevated UV-B conditions. In several experiments (e.g., Barnes et al. 1988), mixtures of plants exposed to elevated UV-B radiation have exhibited changes in the balance of competition even though the respective monocultures of these plants did not exhibit particular effects.

If species competition relationship changes occur on a broad scale, it will be one of the most important ecosystem-level consequences of stratospheric ozone reduction, especially in nonagricultural ecosystems. From the ecological point of species competition, for example, even subtle decreases in plant height due to UV-B radiation might be of eventual significance if different species were affected to different degrees, which finally lead to the change of competent balance between species. However, as yet, the underlying mechanisms of changed UV-B level to alter plant species competition relationships are still unclear.

## UV-B effect on decomposition and nutrient cycling

Though sunlight does not penetrate significantly into soils, elevated UV-B radiation can have far-reaching consequences for soil processes, such as decomposition and nutrient cycling. Duguay and Klironomos (2000) pointed out that UV-B radiation has significant direct effects on the decomposition of leaf litter by stimulating photochemical breakdown of compounds, such as lignin, or by the altering the community of decomposer microorganisms and inhibiting microbial decomposition. Several studies (e.g., Johnson et al. 2002; Niemi et al. 2002) indicated that elevated UV-B radiation could induce changes in soil microbial communities and biomass, especially specific microbial communities in close association with roots, as well as alter populations of small invertebrates. These changes have important implications for litters decomposition and mineral nutrient cycling in the soil, and finally acted on the ecosystem stability. For example, through five years field experiments, Staaij et al. (2001) found with supplemental UV-B radiation, fungi that are associated with roots and important for plant nutrition cycling were substantially decreased in quantity. Although this mechanism remains poorly defined, many of these ecosystem-level phenomena appear to be the result of systemic changes in chemical and physical properties of plants and in the nature of root exudates.

## UV-B effect on plant biomass productivity and crop yield

With reduced photosynthesis under elevated UV-B conditions, plant height and leaf area decrease and dry matter production reduces in many plant species. The elevated UV-B radiation generally has negative impacts on growth, yield and quality of some crops such as soybean and winter wheat (Li and Wang 2001). The response varies with different plant species. Some are very sensitive and some are least sensitive. For example, Feng et al. (2007) found that elevated UV-B radiation, similar to drought stress, could decrease the net photosynthetic capacity of spring wheat through different paths, and led to the reduction of root, stem and leaves biomass and yield, as well as changed biomass and the harvest index.

Many studies have investigated the possible effects of elevated UV-B radiation on food production of agricultural crops. As reviewed by Kakani et al. (2003), about 35% of the studies reported no effect on dry weight, and a few (5%) studies demon-

strated increases in crop dry matter accumulation, and the differences were probably associated with differences in crop species, genotypes and UV-B radiation doses. For example, in a six year field study of a UV-B-sensitive soybean, Teramura et al. (1990) presented a statistically significant 19%–25% reduction in seed yield in five of the six years under a 25% ozone reduction level. Similarly, approximately one-third of all 16 rice cultivars tested showed a statistically significant decrease in total biomass with increased UV-B radiation in a greenhouses experiment (Teramura et al. 1991). For these sensitive cultivars, leaf area and tiller number were also significantly reduced. Li and Wang (1996) reported that increased UV-B radiation decreased crop yield by affecting both grain number and grain weight. However, contrasting results have also been published, showing no effect on crop biomass and grain yield. For example, with spring wheat under field conditions, Calderini et al. (2008) found that if increases in UV-B radiation take place during the latter stages of the crop cycle, the increases of UV-B radiation will not compromise wheat production systems.

A few recent reports indicated that altered UV-B radiation may influence allocation of biomass to root systems. Root mass increased with the attenuation of solar UV-B radiation in experiments conducted in Greenland (Rinnan et al. 2005) and Tierra del Fuego (Zaller et al. 2002). Ruhland et al. (2005) also reported substantial increases in root mass with reduced UV-B radiation in solar UV-B radiation attenuation experiments using potted plants in Antarctica. However, this phenomenon is not always appeared. For example, similar studies in Finland with two mire species indicated an increase in root mass with UV-B radiation supplementation (Rinnan et al. 2006). The underlying mechanisms behind these contradictory responses are not well known.

It is worthy to note that few studies have been undertaken on trees or forests, thought forest production account for up to 80% of global productivity. As we know, only several studies have been done on the relations of trees productivity and UV-B radiation under field conditions. Some studies have demonstrated deleterious effects of UV-B radiation on tree growth and physiology. However, few of these studies were conducted consecutively in multi-year scale, thus the long-term effects of UV-B radiation on trees is unknown. Sullivan (2005) investigated the responses of 35 species to UV-B radiation in North America, and no evidence was found that the expected levels of UV-B enhancement would result in direct losses in productivity, thought 1/3 of these have demonstrated some deleterious effects of elevated UV-B radiation. Field studies with loblolly pine trees showed a decreased photosynthetic activity under simulated ozone depletion scenarios (Teramura and Sullivan 1991). Similar effects are reported for plants from alpine and high latitude environments, such as spruce, birch and ash. The preliminary results suggested that elevated UV-B effects are normally more severe in conifers than in deciduous species.

## Concluding remarks

A great variety of physiological and morphological plant responses to UV-B radiation have been demonstrated over the past thirty years. The information is helpful in understanding common responses of plants to UV-B radiation, such as diminished growth, acclimation responses of plants to UV-B radiation and interactions of plants with consumer organisms such as insects and plant pathogens. Results collected in this review suggest that approximately two out of three terrestrial plant species appear to be susceptible to increased UV-B radiation, and most evidences indicate that elevated UV-B irradiation is usually detrimental. However, the responses of terrestrial plants to elevated UV-B radiation are fairly complex, due to the complex terrestrial system. Our current knowledge of this subject is too limited to draw any specific conclusions, but the following general conclusions can be draw based on this review.

(1) UV-B radiation can alter plant morphology through reductions in plant height and leaf area and increase in leaf thickness, and changes in plant geometry.

(2) UV-B radiation can reduce biomass production and seed yield through reductions in leaf photosynthesis and plant growth; plant physiological processes are influenced by elevated UV-B radiation. Photosynthesis is often suppressed, and the production of plant secondary metabolites is increased.

(3) Several environmental factors have been shown to modify UV-B induced responses of plants, either ameliorating or enhancing the UV-B radiation effect, while in turn UV-B radiation can alter the way in which plants respond to other factors such as water stress.

(4) UV-B-induced changes in soil microbial communities and biomass, as well as altered populations of small invertebrates have important implications for processing of nutrient cycling in the soil.

In general, there have been significant advances in our understanding of the effects of UV-B radiation on terrestrial plants. However, assessment of the biological effects of UV-B is not simple; because there exists variability between species and varieties in their sensitivity to UV-B radiation and in their ability to acclimate. Practically, most of the studies were conducted with presumed UV-B levels to simulate conditions that would exist with a defined reduction in the ozone layer (typically 10% to 20%). Although many plant responses to UV radiation have been reported, complete mechanistic details of these responses have not been elucidated. These responses, such as biomass reductions or changes in the ability of crop plants to compete with weeds, could result from any UV-B induced events: DNA damage, direct photosynthetic damage, membrane changes, protein destruction, or hormone inactivation. Based on these, further studies are suggested to be conducted in the future as follow:

(1) To determine the direct and indirect effects of elevated UV-B radiation on ecosystem processes, and the ultimately interactive effect of UV-B radiation with other environmental factors on plants and the ecosystem;

(2) To examine the mechanisms of plants respond to UV-B radiation, and the dose-response relationships;

(3) To identify the possible strategies for mitigating, or adapting to reduce the impacts of UV-B change on terrestrial plants, especially economically important crops. This will be a major goal of future research subject to maintain agricultural production and ecosystem stability.

## References

Alexieva V, Sergiev I, Mapelli S, Karanov E. 2001. The effect of drought and

ultraviolet radiation on growth and stress markers in pea and wheat. *Plant, Cell & Environment*, **24**: 1337–1344.

Andersson B, Styring S. 1991. Photosystem II: molecular organization, function, and acclimation. In: *Current topics in bioenergetics*, (Lee CP. ED.) Vol. 16. London: Academic Press, pp. 1-81.

Ballaré CL, Barnes PW, Flint SD, Price S. 1995. Inhibition of hypocotyl elongation by ultraviolet-B radiation in de-etiolating tomato seedlings. Ⅱ. Time-course, comparisons with flavonoid responses, and adaptive significance. *Physiologia Plantarum*, **93**: 593–601.

Ballaré CL, Scopel AL, Stapleton AE, Yanovsky MJ.1996. Solar ultraviolet-B radiation affects seedling emergence, DNA integrity, plant morphology, growth Rate, and attractiveness to herbivore insects in *Datura ferox*. *Plant Physiology*, **112**(1): 161–170.

Barnes PW, Jordan PW, Gold WG, Flint SD, Caldwell MM. 1988. Competition, morphology and canopy structure in wheat and wild oat exposed to elevated ultraviolet-B radiation. *Functional Ecology*, **2**: 319–330.

Battaglia PR, Brennan TM. 2000. Differential effects of short-term expose to ultraviolet-B radiation upon photosynthesis in cotyledons of a resistant and a susceptible species. *International Journal of Plant Sciences*, **161**: 771–778.

Becwar MR, Moore FD, Burke MJ. 1982. Effects of deletion and enhancement of ultraviolet-B (280-315 nm) radiation on plants grown at 3000 m elevation. *Journal of the American Society for Horticultural Science*, **107**: 771–779.

Beggs CJ, Stolzer-Jehle A, Wellmann E. 1985. Isoflavonoid formation as an indicator of UV-stress in bean (*Phaseolus vulgaris* L.) leaves. *Plant Physiology*, **79**: 630–634.

Bergo E, Segalla A, Giacometti GM, Tarantino D, Soave C, Andreucci F, Barbato R. 2003. Role of visible light in the recovery of photosystem II structure and function from ultraviolet-B stress in higher plants. *Journal of Experimental Botany*, **54**: 1665–1673.

Bornman JF, Vogelman TC. 1991. Effect of UV-B radiation on leaf optical properties measured with fiber optics. *Journal of Experimental Botany*, **41**: 547–554.

Britt AB. 1995. Repair of DNA damage induced by ultraviolet radiation. *Plant Physiology*, **108**: 891–896.

Cai Xian, Peng Shaolin, Xia Hanping. 2007. Growth and Photosynthetic Responses of Different Successional Tree Species in Low Subtropics to Elevated UV-B Radiation in the Field. *Acta Scientiarum Naturalium Universitatis Sunyatseni*, **46**(2): 72–76. (in Chinese)**.**

Calderini DF, Lizana XC, Hess S, Jobet CR, Zuniga JA. 2008. Grain yield and quality of wheat under increased ultraviolet radiation (UV-B) at later stages of the crop cycle. *Journal of Agricultural Science*, **146**: 57–64.

Caldwell MM, Bjorn LO, Bornmann JF, Flint SD, Kulandaivelu G, Teramura AH, Tevini M. 1998. Effects of increased solar UV-B on terrestrial ecosystems. *Journal of Photochemistry and Photobiol*ogy. B: Biology, **46**: 40–52.

Caldwell MM, Bornman JF, Ballaré CL, Flint SD, Kulandaivelu G. 2007. Terrestrial ecosystems, increased solar ultraviolet radiation, and interactions with other climate change factors. *Photochemical & Photobiological Sciences*, **6**(3): 252–266.

Caldwell MM, Teramura AH, Tevini M, Bornman JF, Bjorn LO, Kulandaivelu G. 1995. Effects of increased solar ultraviolet radiation on terrestrial plants. *Ambio*, **24**: 166–173.

Caldwell MM. 1971. Solar UV irradiation and the growth and development of higher plants. In: Giese AC (Ed.), *Photophysiology*, vol. 6. New York: Academic Press.

Chimphango SBM, Musil CF, Dakora FD. 2004. Responses to ultraviolet-B radiation by purely symbiotic and $NO_3$-fed nodulated tree and shrub legumes indigenous to southern Africa, *Tree Physiology*, **24**: 181–192.

Convey P, Pugh PJA, Jackson C, Murray AW, Ruhland CT, Xiong FS, Day TA. 2002. Response of Antarctic terrestrial microarthropods to long-term climate manipulations. *Ecology*, **83**: 3130–3140.

Correia CM, Areal ELV, Torres-Pereira MS, Torres-Pereira JMG. 1999. Intraspecific variation in sensitivity to ultraviolet-B radiation in maize grown under field conditions. II. Physiological and biochemical aspects. *Field Crops Research*, **62**: 97–105.

Correia CM, Moutinho JM, Pereira JF, Countinho Björn LO, Torres-Pereira JMG. 2005, Ultraviolet-B radiation and nitrogen affect the photosynthesis of maize: a Mediterranean field study, *European journal of agronomy*, **22**: 337–347.

Duguay KJ, Klironomos JN. 2000. Direct and indirect effects of elevated UV-B radiation on the decomposing and competitive abilities of saprobic fungi. *Applied soil ecology*, **14**: 157–164.

Dunning CA, Chalker-Scott L, Scott JD. 1994, Exposure to ultraviolet-B radiation increases cold hardiness in Rhododendron. *Physiologia Plantarum*, **92**: 516–520.

Feng Huyuan, An Lizhe, Chen Tuo, Qiang Weiya, Xu Shijian, Zhang Manxiao, Wang Xunling. 2002. Intraspecific difference of soybean in response to elevated UV-B radiation. *Acta Botanica Boreali-Occidentalia Sinica*, **22**(4): 845–850. (in Chinese) .

Feng HY, Li SW, Xue LG, An LZ, Wang XL. 2007. The interactive effects of elevated UV-B radiation and soil drought on spring wheat. *South African Journal of Botany*, **73**(3): 429–434.

Han R, Wang XL, Yue M. 2002. Influence of He-Ne laser irradiation on the excision repair of cyclobutyl pyrimidine dimers in the wheat DNA. *Chinese Science Bulletin*, **47**(10): 818–827.

Hofmann RW, Campbell BD, Fountain DW, Jordan BR, Greer DH, Hunt DY, Hunt CL. 2001. Multivariate analysis of intraspecific responses to UV-B radiation in white clover (*Trifolium repens* L.). *Plant, cell and environment*, **24**: 917–927.

Holmes. 1997. Action spectra for UV-B effects on plants: monochromatic approaches for analyzing plant responses. In: Lumsden, P.J., (Ed.), Plants and UV-B: Responses to Environmental Change. Cambridge University Press, Cambridge, pp. 31–50.

Hunt, JE, McNeil DL. 1998. Nitrogen status affects UVB sensitivity of cucumber. *Australian Journal of Plant Physiology*, **1**: 79–86.

Johnson D, Campbell CD, Lee JA, Callaghan TV, Gwynn-Jones D. 2002. Arctic microorganisms respond more to elevated UV-B radiation than $CO_2$. *Nature*, **416**: 82–83.

Johnston HS. 1971. Reduction of stratospheric ozone by nitrogen oxide catalysts from supersonic transport exhaust. *Science*, **173**: 517–522.

Kakani VG, Reddy KR, Zhao D, Mohammed AR. 2003. Ultraviolet-B radiation effects on cotton (*Gossypium hirsutum*) morphology and anatomy. *Annals of Botany*, **91**: 817–826.

Kakani VG, Zhao KRR, Sailaja DK. 2003. Field crop responses to ultraviolet-B radiation: a review. *Agricultural and Forest Meteorology*, **120**: 191–218.

Kimura S, Sakaguchi K. 2006. DNA repair in plants. *Chemical Reviews*, **106**: 753–766.

Koti S, Reddy KR, Reddy VR, Kakani VG, Zhao D. 2005. Interactive effects of carbon dioxide, temperature, and ultraviolet-B radiation on soybean (*Glycine max* L) flower and pollen morphology, pollen production, germination, and tube lengths. *Journal of Experimental Botany*, **56**: 725–736.

Kumagai T, Hidema J, Kang H-S, Sato T. 2001. Effects of supplemental UV-B radiation on the growth and yield of two cultivars of Japanese lowland rice (*Oryza sativa* L.) under the field in a cool rice-growing region of Japan. *Agriculture, Ecosystems and Environment*, **83**: 201–208.

L'Hirondell S, Binder WD. 2005. Temperature stress tolerance of conifer seedlings after exposure to UV-B radiation. *Photochemistry and photobiology*, **81**: 1094–1100.

Li J, Ou-Lee TM, Raba R, Amundson RG, Last RL. 1993. Arabidopsis flavonoid mutants are hypersensitive to UV-B irradiation. *The Plant Cell*, **5**(2): 171–179.

Li Yuan, Wang Xunling. 1996. The effect of elevated UV-B radiation on the physiological indicator, yield and quality of wheat. *Acta Scientiae Circumstantiae*, **18**(5): 504–509. (in Chinese)**.**

Li Yuan, Wang Xunling. 2001. Effects of elevated UV-B radiation on population quantity dynamics of weeds, soil macroanimals and wheat aphids in the wheat field ecosystem. *Acta Ecologica Sinica*, **21**(1):131–135. (in Chinese).

Li Yuan, Yue Ming, Wang Xunling. 1998. Effects of elevated ultraviolet-B radiation on crop structure, growth and yield components of spring wheat under field conditions. *Field Crops Research*, **57**(3): 253–263.

Machado CR, Oliveira RL, Boiteux S, Praekelt UM, Meacock PA, Menck CF.

1996. A thiamine biosynthetic gene in Arabidopsis thaliana complements bacterial defects in DNA repair. *Plant Molecular Biology*, **31**: 585–593

Mark U, Tevini M. 1996. Combination effects of UV-B radiation and temperature on sunflower and maize seedlings. *Journal of plant physiology*, **148**: 49–56.

Mazza CA, Zavala J, Scopel AL, Ballaré CL. 1999. Perception of solar UVB radiation by phytophagous insects: behavioral responses and ecosystem implications. *Proceedings of the National Academy of Sciences (USA)*. **96**: 980–985.

Nedunchezhian N, Kulandaivelu G. 1996. Effects of ultraviolet-B elevated radiation and temperature on growth and photochemical activities in Vigna unguiculata. *Biologia Plantarum*, **38**: 205–214.

Niemi R, Martikainen PJ, Silvola J, Wulff A, Turtola S, Holopainen T. 2002. Elevated UV-B radiation alters fluxes of methane and carbon dioxide in peatland microcosms, *Global Change Biology*, **8**: 361–371.

Olsson LC, Veit M, Weissonbock G, Bornmann JF. 1998. Differential flavonoid response to elevated UV-B radiation in Brassica napus. *Phytochemistry*, **4**: 1021–1028.

Olszuk D.1996. UV-B effect on crops: response of the irrigated rice ecosystem. *Journal of plant physiology*. **148**: 24–26.

Paoletti E. 2005. UV-B and Mediterranean forest species: direct effects and ecological consequences. *Environmental pollution*, **137**(3): 372–379.

Paul ND. 2000. Stratospheric ozone depletion, UV-B radiation and crop disease. *Environmental pollution*, **108**: 343–355.

Post A, Lukins PB, Walker PJ, Larkum AWD. 1996. The effects of ultraviolet irradiation on P680+ reduction in PS II core complexes measured for individual S-states and during repetitive cycling of the oxygen-evolving complex, *Photosynthesis Research*. **49**:21–27.

Qaderi MM, Reid DM. 2005. Growth and physiological responses of canola (*Brassica napus*) to UV-B and $CO_2$ under controlled environment conditions, *Physiologia Plantarum*, **125**: 247–259.

Qi Z, Yue M, Hang R, Wang XL. 2002. The Damage Repair Role Of He-Ne Laser In Plant Exposed To Different Intensities Of Ultraviolet-B Irradiation. *Photochemistry and Photobiology*, **75** (6): 680–686.

Qi Z, Yue M, Wang XL. 2000. Laser pretreatment protects cells of broad bean from UV-B radiation damage. *Journal of photochemistry and photobiology (B: Biology)*, **57**: 60–65.

Qiu ZB, Zhu XJ, Li FM, Liu X, Yue M. 2007. The optical effect of semiconductor laser on protecting wheat from UV-B radiation damage. *Photochemical and Photobiological Science*, **6**: 788−793.

Ren J, Dai WR, Xuan ZY, Yao YN, Korpelainen H, Li CY. 2007. The effect of drought and elevated UV-B radiation on the growth and physiological traits of two contrasting poplar species. *Forest Ecology and Management*, **239**(1-3): 112–119.

Ries G, Heller W, Puchta H, Sandermann H, Seidlitz HK, Hohn B. 2000. Elevated UV-B radiation reduces genome stability in plants. *Nature*, **406**: 98−101.

Rinnan R, Gehrke C, Michelsen A. 2006. Two mire species respond differently to elevated ultraviolet-B radiation: Effects on biomass allocation and root exudation, *New Phytologist*, **169**: 809−818.

Rinnan R, Keinanen MM, Kasurinen A, Asikainen J, Kekki TK, Holopainen T, Ro-Poulsen H, Mikkelsen TN, Michelsen A. 2005. Ambient ultraviolet radiation in the Arctic reduces root biomass and alters microbial community composition but has no effects on microbial biomass. *Global Change Biology*, **11**: 564–574.

Rousseaux MC, Ballaré CL, Giordano CV, Scopel AL, Zima AM, Szwarcberg-Bracchita M, Searles PS, Caldwell MM, Díaz SB. 1999. Ozone depletion and UVB radiation: Impact on plant DNA damage in southern South America. *Proceedings of the National Academy of Sciences (USA)*, **96**: 15310–15315.

Ruhland CT, Xiong FS, Clark WD, Day TA. 2005. The influence of ultraviolet-B radiation on growth, hydroxycinnamic acids and flavonoids of *Deschampsia antarctica* during springtime ozone depletion in Antarctica. *Photochemistry and Photobiology*, **81**: 1086−1093.

Sedej TT, Gaberscik A. 2008. The effects of elevated UV-B radiation on physiological activity and growth of Norway spruce planted outdoors over 5 years. *Trees-Structure and Function*, **22**(4): 423−435.

Sicora, C, Mate Z, Vass I. 2003. The interaction of visible and UV-B light during photodamage and repair of Photosystem II. *Photosynthesis Research*, **75**: 127−137.

Steinmuller D, Tevini M. 1985. Action of ultraviolet radiation (UV-B) upon cuticular waxes in some crop plants. *Planta,* **164**: 557–564.

Sullivan JH. 2005. Possible impacts of changes in UV-B radiation on North American trees and forests. *Environmental Pollution*, **137**: 380–389.

Teklemariam T, Blake TJ. 2003. Effects of UVB preconditioning on heat tolerance of cucumber (*Cucumis sativus* L.). *Environmental and experimental botany*, **50**: 169-182.

Teklemariam T, Blake TJ. 2004. Phenylalanine ammonia-lyase-induced freezing tolerance in jack pine (*Pinus banksiana*) seedlings treated with low, ambient levels of ultraviolet-B radiation, *Physiologia Plantarum*, **122**: 244−253.

Teramara AH. 1990. Interaction of elevated UV-B radiation and $CO_2$ on productivity and photosynthetic characteristic in wheat rice and soybean. *Plant Physiology*, **94**:470–475.

Teramura AH, Sullivan JH, Lydon J. 1990. Effects of solar UV-B radiation on Soybean yield and seed quality: a six-year field study. *Physiologia Plantarum*, **80**: 5−11.

Teramura AH, Sullivan JH. 1991. Potential effects of increased solar UV-B on global plant productivity. pp. 625−634. In Riklis E (ed.) Photobiology, Plenum Press, New York.

Terarnura AH. 1983. Effects of ultraviolet-B radiation on the growth and yield of crop plants. *Physiologia Plantarum*, **58**: 415−422.

Tevini M, Mark U, Fieser G, Saile M. 1991. Effects of elevated solar UV-B radiation on growth and function of selected crop plant seedlings. In: Riklis E (ed.), *Photobiology,* pp. 635-649., New York: Plenum Publishers,.

van de Staaij JWM, Rozema J, van Beem A, Aerts R. 2001. Increased solar UV-B radiation may reduce infection by arbuscular mycorrhizal fungi (AMF) in dune grassland plants: Evidence from five years of field exposure. *Plant Ecology*, **154**:171−177.

Vass I, Sass L, Spetea C, Bakou A, Ghanotakis D, Petrouleas V. 1996. UV-B induced inhibition of Photosystem II electron transport studied by EPR and chlorophyll fluorescence. Impairment of donor and acceptor side components, *Biochemistry*, **35**: 8964–8973.

World Meteorological Organization (WMO). 2007, Scientific Assessment of Ozone Depletion: 2006, Global Ozone Research and Monitoring Project - Report No. **50**, pp572, Geneva.

Yamasaki S, Noguchi N, Mimaki K. 2007. Continuous UV-B Irradiation Induces Morphological Changes and the Accumulation of Polyphenolic Compounds on the Surface of Cucumber Cotyledons. *Journal of Radiation Research*, **48**: 443−454.

Yang X, Heisler GM, Montgomery ME, Sullivan JH, Whereat EB, Miller DR. 1995. Radiative properties of hardwood leaves to ultraviolet irradiation. *International Journal of Biometeorology*, **38**: 60−66.

Yang Y, Yao Y, Xu G, Li C. 2005. Growth and physiological responses to drought and elevated ultraviolet-B in two contrasting populations of *Hippophae rhamnoides*. *Physiologia Plantarum*, **124**: 431−440.

Zaller JG, Caldwell MM, Flint SD, Scopel AL, Sala OE, Ballaré CL. 2002. Solar UV-B radiation affects below-ground parameters in a fen ecosystem in Tierra del Fuego, Argentina: Implications of stratospheric ozone depletion. *Global Change Biology*, **8**: 867–871.

Zavala JA, Scopel AL, Ballaré CL. 2001. Effects of ambient UV-B radiation on soybean crops: Impact on leaf herbivory by Anticarsia gemmatalis, *Plant Ecology*, **156**: 121−130.

Zhao D, Reddy KR, Kakani VG, Mohammed AR, Read JJ, Gao W. 2004. Leaf and canopy photosynthetic characteristics of cotton (*Gossypium hirsutum*) under elevated $CO_2$ concentration and UV-B radiation. *Journal of Plant Physiology*, **161**: 581–590.

Zhao D, Reddy KR, Kakani VG, Read J, Sullivan J. 2003. Growth and physiological responses of cotton (*Gossypium hirsutum* L.) to elevated carbon dioxide and ultraviolet-B radiation under controlled environment conditions. *Plant*, *Cell & Environment*, **26**(5): 771–782.